

SEXUAL DIMORPHISM AND ECOLOGICAL DIFFERENTIATION OF MALE AND FEMALE PLANTS¹

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ABSTRACT

The evolution of dioecy within a plant population introduces a situation in which there is divergent selection for means of achieving reproductive success. Male and female individuals play different roles in the reproductive biology of a dioecious species and hence have very different resource demands imposed upon them. The selection pressures presented by these different resource demands could in turn lead to the evolution of sexual dimorphism. Empirical studies of several dioecious plant species have shown that male and female plants differ in their resource allocation patterns. These differences between the sexes have also been shown to lead to sexual dimorphism in a wide range of life history characteristics in the dioecious perennial *Chamaelirium luteum*, including age at first reproduction, flowering schedules, size and size dynamics, and mortality rates. Quantitative genetic studies of resource allocation patterns for *C. luteum* suggest that the observed sexual dimorphism is probably the result of independent selection on the two sexes separately rather than the result of selection specifically favoring sexual dimorphism.

The establishment of a stable genetic polymorphism that results in separate male and female individuals is just the first step in the evolution of sexual dimorphism. The two sexes, by virtue of attaining reproductive success in different ways, play distinct roles in the biology of a species. Thus, a genetic polymorphism for sex expression is likely to have a wide range of ecological consequences, which in turn could result in selection pressures that may eventually lead to the evolution of secondary differences between the sexes. Secondary differences that have been observed between male and female individuals within dioecious species have included morphological, ecological, and behavioral attributes and are often referred to collectively by the phrase "sexual dimorphism."

Studies on animal species have shown that sexual dimorphism is evident in almost every aspect of their ecology and evolution (for reviews, see Selander, 1972; Maynard Smith, 1978; O'Donald, 1980). Traditional studies on sexual dimorphism in plants have been limited largely to floral characteristics (for review, see Lloyd & Webb, 1977); but, over the past few years, there has

been a growing interest in broader manifestations of sexual dimorphism in plants (e.g., Lloyd & Webb, 1977; Grant & Mitton, 1979; Onyekwelu & Harper, 1979; Wallace & Rundel, 1979; Hancock & Bringham, 1980; Bullock & Bawa, 1981; Bullock et al., 1982; Meagher & Antonovics, 1982a, 1982b). This has included extensive discussion of various factors involved in the evolution of dioecy (e.g., Bawa & Opler, 1975; Lloyd, 1976, 1979; Charlesworth & Charlesworth, 1979), but there is still relatively little known about the evolution of sexual dimorphism in plants beyond the differentiation of sex function.

Clearly the two sexes within a dioecious plant species perform very different functions in reproduction. As a consequence of these different functions, the two sexes may be subject to different sorts of resource demands (Lloyd, 1979; Charlesworth & Charlesworth, 1981; Charnov, 1982; Meagher & Antonovics, 1982a, 1982b) and, in turn, to divergent selection pressures, which will act to enhance the evolution of sexual dimorphism. In fact, observed cases of sexual dimorphism in traits related to life history and resource allocation (Lawrence, 1963, 1964;

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Bouwkamp & McCully, 1972; Putwain & Harper, 1972; Brockman & Bocquet, 1978; Lovett Doust & Harper, 1980; Gross & Soule, 1981; Meagher & Antonovics, 1982b) are presumably related to differential selection pressures that are imposed on male and female plants.

However, the extent of sexual dimorphism and the rate at which it is likely to evolve are subject to a variety of ecological and genetical constraints. For example, in order to remain a sexually reproducing species, male and female plants must maintain sufficient overlap in their ecological tolerances and life history characteristics to be able to interbreed effectively. This ecological limitation may be overcome by species with apomictic female plants (cf. Gustafsson, 1946–1947, cited in Grant, 1971). Genetical constraints arise because male and female individuals are members of the same species, and hence are limited in the extent that they can undergo genetically based divergence due to the overlap in genes in their respective genomes and the resultant genetic correlations (Lande, 1980). Thus the evolution of sexual dimorphism embodies the balance between factors acting to promote change and constraints tending to restrict change within populations.

The present paper addresses the processes and constraints involved in the evolution of sexual dimorphism in plants through an analysis of the dioecious perennial *Chamaelirium luteum* (Liliaceae). The population biology of this species has been well studied (Meagher, 1980, 1981, 1982; Meagher & Antonovics, 1982a, 1982b) and *C. luteum* has been shown to have extensive sexual dimorphism both in its overall morphology and in various life history characteristics. The discussion below will draw on investigations of four naturally occurring populations in the piedmont of North Carolina designated as *Natural Area*, *Seawell*, *Silver Hill*, and *Botanical Garden*; precise locations and site descriptions are given in Meagher (1980). Experimental analyses discussed below are based upon use of seed collected from three of these sites. Seed collected by common pistillate parent (halfsibship) were planted out and raised in the Duke University Phytotron. Altogether, 30 seedlings representing 30 halfsibships (900 total individuals) were planted. These plants were taken through a series of induction cycles (low temperature, short photoperiod) to promote flowering. The specific growth condi-

tions and results of studies on the sex ratio are described in Meagher (1981).

The discussion that follows will focus on the following questions. How does sexual dimorphism influence the breeding structure of a population? What are the ecological consequences of sex differentiation? What are the genetic bases of sexual dimorphism and the probable selective forces that lead to the evolution of sexual dimorphism? Finally, what is the nature of ecological and genetic constraints imposed on the evolution of sexual dimorphism?

SEX RATIO AND SPATIAL DISTRIBUTION OF MALE AND FEMALE PLANTS

Aside from separation of the sexes into distinct individuals, there are other ways in which sex differentiation affects breeding relationships and the reproductive behavior of male and female plants. For example, the relative numbers of male and female plants, the sex ratio, has an influence on the effective population size (e.g., Ewens, 1969: 32–36). Also, if there is a strong numerical excess of one sex, the genetic contribution per individual of that sex will be correspondingly lower than that for individuals of the other sex. Finally, if differences between the sexes are sufficient to lead to noticeable differences in ecological tolerances, there may result a tendency for male and female plants to occur in different microhabitats, leading to increased spatial separation of the sexes.

A particularly striking feature of populations of *Chamaelirium luteum* is that the flowering sex ratios are extremely male biased (Meagher, 1981). If one observes the sex ratio among flowering plants during the breeding season in any given year, there is a large excess of male plants (Table 1). However, because only a relatively small percentage of the plants in a population flower in a given year, estimates of sex ratios based on a single flowering season could be biased by differences between male and female plants in their flowering schedules. There is a great deal of year to year variation in flowering sex ratios within any one site, showing that differential flowering behavior between male and female plants can have a dramatic effect on sex ratio estimates for any one season. In the present study, individual plants were monitored over a series of flowering seasons, so that for each successive year it was possible to obtain a cumulative estimate of the population sex ratio based not only on the plants

TABLE 1. Sex ratios in four populations of *Chamaelirium luteum* (from Meagher, 1981). Flowering sex ratios (male/female) are given for 1974–1979; G^2 (1 degree of freedom) test results for departure from a one to one sex ratio were statistically significant for all flowering sex ratios.

Site	Year	Percent of Population in Flower	Flowering Sex Ratio	Cumulative Sex Ratio Estimate
Natural Area (N \cong 2,200)	1974	9.7	4.51	
	1975	10.6	3.07	
	1976	13.3	5.30	
	1977	19.9	3.41	2.47
	1978	6.7	4.52	
	1979	3.6	10.57	
	1980	11.0	3.90	
Seawell (N \cong 949)	1975	16.2	7.11	
	1976	14.0	6.00	
	1977	14.6	4.79	3.37
	1978	9.5	6.50	
	1979	1.6	14.00	
	1980	25.0	4.39	
Botanical Garden (N \cong 450)	1975	25.1	2.80	
	1976	19.1	3.47	
	1977	27.8	3.47	1.76
	1978	15.8	2.89	
	1979	15.6	3.38	
	1980	38.9	2.37	
Silver Hill (N \cong 1,103)	1975	12.5	3.18	
	1976	9.0	3.71	1.74
	1977	19.1	2.52	
	1978	5.9	2.82	

in flower in a given year, but also on plants that had flowered previously. Inspection of such cumulative estimates showed a monotonic decline as the number of successive flowering seasons considered increased (Meagher, 1981). These cumulative estimates leveled off after the first several years and showed that the sex ratios for these four populations do show an overall excess of male plants (Table 1), even though this excess is generally not as dramatic as that observed within a single flowering season.

One can also look at the distribution of sex ratios over different microgeographic subunits of a population as a means of assessing the relative spatial distributions of male and female plants within a population. Tests of within population heterogeneity in sex ratio (Fig. 1) indicate that the sex ratio is not uniform within natural populations but rather varies from subunit to subunit, reflecting an underlying differential spatial distribution of male and female plants. Differences between male and female individuals of *C.*

luteum in their relative spatial distributions within a population have been confirmed in a number of statistical analyses (Meagher, 1980; Meagher & Burdick, 1981).

The above discussion outlines a range of ecological consequences of dioecy. The differences between flowering sex ratios and cumulative estimates of the overall population sex ratios of *Chamaelirium luteum* suggest that male and female plants show different types of flowering behavior. The tendency toward differential distribution of male and female plants over different microsites, presumably the consequence of differential survivorship of the two sexes over these different microsites, provides evidence of ecological differentiation between the sexes. These phenomena are both related to the life history characteristics of the two sexes in terms of reproductive activity and survivorship. Therefore a comparative examination of the life histories of male and female plants provides a useful means for obtaining insight into such ecological side effects of sex differentiation.

NATURAL AREA

	3/0	3/0	1/4		16/6	5/1	
1/1	28/18	18/3	19/12	8/2	53/18	90/21	14/4
3/1	63/24	20/14	22/8	16/11	57/28	28/21	
3/1	21/6	3/3	0/1	28/14	28/5	9/1	

BOTANICAL GARDEN

			1/5	0/1		
		2/0	7/1	2/1		
			6/5	6/2	2/0	
			6/0	4/8	13/3	
	1/0		0/1	4/2	4/1	0/1
				0/2	3/0	17/10
2/1	6/7				1/0	2/2
11/5	8/3	2/0	3/0		1/0	1/0
0/1	13/7	8/8			0/2	
		1/0	2/0		1/0	8/7
			4/0			1/1

SILVER HILL

4/2	21/12	11/9	0/1
4/2	21/15	38/17	
23/2	27/12	27/12	1/0
8/7	38/13	5/4	

SEAWELL

38/5	36/8	11/6	6/0
45/9	67/27	10/0	
29/3	17/8	1/0	
2/0	0/3		

FIGURE 1. Within site heterogeneity in sex ratio (male/female) in *C. luteum* (from Meagher, 1980). G^2 test results indicated significant heterogeneity for the Natural Area ($P < 0.05$), Seawell ($P < 0.005$), and Botanical Garden ($P < 0.005$) sites (Meagher, 1980).

LIFE HISTORY DIFFERENCES BETWEEN MALE AND FEMALE PLANTS

The effect of sexuality on life history characteristics can be conveniently illustrated by moving temporally through the lifespans of the two sexes. The first aspect of life history considered here is the age at first reproduction (Fig. 2). These ages at first reproduction are based on the number of successive induction cycles to which a plant was exposed before it flowered for the first time among the cohorts of plants raised in the Duke University Phytotron. Clearly, male plants were inclined to begin flowering at an earlier age than female plants.

Various features of the sex ratio of *C. luteum* discussed above suggest that, among sexually mature individuals, male and female plants differ in their flowering schedules. The flowering schedules of male and female plants are compared here by considering the number of times plants of a given sex flowered over a span of years

(Table 2). Male plants flowered more frequently than did female plants. An alternative way of stating these results is that female plants tend to have longer intervals between flowering episodes than do male plants.

Once an individual of *C. luteum* becomes established, its size, measured as the number of rosette leaves, plays an important role in determining its subsequent life history behavior (Meagher, 1982). The number of rosette leaves on female plants tends to be greater than the number of rosette leaves on male plants (Table 3), indicating that female plants are, on average, larger than male plants. Furthermore, the impact of flowering on the resource status of an individual is reflected in the year to year change in rosette leaf number. Percentage changes in the number of rosette leaves from the year before to the year after flowering were estimated for male and female plants (Table 4), and there was a significant reduction in size among plants that had flowered, suggesting that flowering imposed

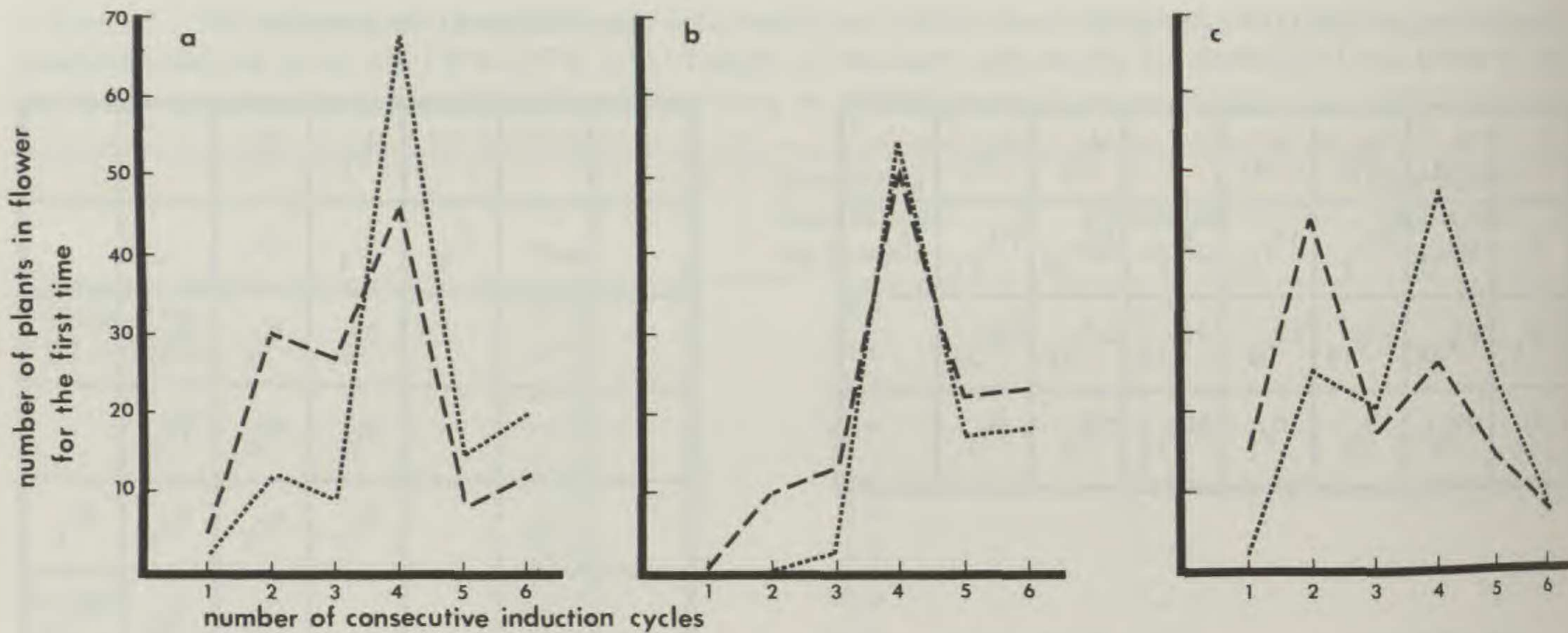


FIGURE 2. Age at first reproduction for male (dashed line) and female (dotted line) seedlings in the Duke University Phytotron; sites of origin for the seed are Natural Area (a), Silver Hill (b), and Botanical Garden (c).

a substantial drain on the resources of an individual. This effect was much more pronounced for female than it was for male plants.

The final stage in the life history to consider is death. Cumulative estimates of annual mortality rates for the two sexes (Table 5) show that female plants had a higher mortality rate than did male plants in two of three sites. For one of these two sites, the female mortality rate was significantly higher than the male mortality rate.

When these various life history characteristics of male and female plants are considered collectively, an overall pattern emerges that indicates a higher resource cost of flowering for female plants. With a later age at first reproduction and longer intervals between flowering episodes, female plants could be delaying flowering until they have assimilated a sufficient resource base to flower successfully. The tendency of female plants to be larger than male plants is also suggestive of a higher resource "threshold" that may be necessary for flowering to occur. In other words, female plants may delay flowering until they have achieved a greater size and are hence better buffered against the proportionately greater resource depletion that flowering represents for them. Finally, the extra costs and consequent resource depletion brought on by flowering for female plants could expose them periodically to a higher risk of mortality, resulting in a relatively higher mortality rate for female plants.

It seems quite reasonable that many of the observed life history differences between the sexes are causally related to the specific male and fe-

male resource demands and resource allocation patterns. From an evolutionary standpoint, therefore, one would expect that male and female plants would have very different types of selection pressures imposed on their resource allocation patterns. There may be divergent selection that favors male plants that put a relatively low proportion of their resources into flowering and that flower more frequently and that favors female plants that put a relatively high proportion of their resources per flowering episode into less frequent flowering.

RESOURCE ALLOCATION AND THE EVOLUTION OF SEXUAL DIMORPHISM

Traits or characters associated with sexual dimorphism, such as differences in resource allocation, are quantitative rather than qualitative in nature. The genetic basis of such characters is best defined by quantitative genetics models in which genetic variation is presumed to result from allelic variation at a large number of loci, each of which makes a small additive contribution to the overall expression of the trait under study (Falconer, 1981; Mather & Jinks, 1982). The genetic and evolutionary behavior of such quantitative variation can thus be studied by the application of appropriate statistical methods.

The phytotron studies described above were based on half-sibships of seedlings; information collected on quantitative characters from sets of half-sibships can be employed in the estimation of genetic parameters. Following the fourth in-

TABLE 2. The percentage of plants in flower in a given season that last flowered X years ago. These percentages represent averages over all consecutive years for which flowering data had been obtained through 1980 (see Meagher, 1981).

Site	X	Male Plants	Female Plants
Natural Area	1	37.4	1.6
	2	22.9	17.8
	3	12.0	19.0
	4	2.1	14.2
	5	2.2	6.0
	6	1.5	0.0
Seawell	1	30.1	0.0
	2	33.0	7.8
	3	18.3	8.3
	4	5.7	8.0
	5	7.3	11.4
Silver Hill	1	32.7	7.7
	2	34.1	17.2
	3	4.2	17.7

duction cycle in the phytotron, male and female plants within 22 of the 30 half-siblings were in flower for the first time and plants were harvested for dry weight measurements of three vegetative and three reproductive structures (Table 6). It is interesting to note that although male plants had a proportionately greater dry weight in their vegetative parts than did female plants, all of the structures on female plants had a higher absolute dry weight. Even though all plants were the same age, the female plants were on average larger than the male plants.

Dry weight values were log-transformed and percent dry weight values were subjected to arcsin square root transformations prior to statis-

TABLE 3. Rosette leaf number for male and female plants of *Chamaelirium luteum*. Values presented are from 1975–1979 pooled; cumulative numbers of observations for each sex are given in parentheses. Male and female means within each site were compared using an ANOVA (Sokal & Rohlf, 1969), and all three pairs of means are significantly different ($P < 0.0001$).

Site	Male Plants	Female Plants
Natural Area	4.1 (2,492)	4.4 (1,014)
Seawell	4.4 (1,025)	4.9 (260)
Silver Hill	4.9 (628)	5.3 (298)

TABLE 4. Percentage in rosette leaf number from the year before to the year after flowering (year 3–year 1); sample sizes are given in parentheses. Significance tests of departures from 0 were made using a *t* test (Sokal & Rohlf, 1969). Results from *t* tests comparing male transitions and female transitions were all statistically significant ($P < 0.001$).

Site	Male Plants	Female Plants
Natural Area	-17 (247) ^c	-39 (133) ^c
Seawell	-16 (118) ^c	-29 (34) ^c
Silver Hill	+2 (28) ^a	-34 (12) ^b

^a Not significant.

^b $P < 0.05$.

^c $P < 0.001$.

tical analysis because in both cases transformed values showed a better fit to a normal distribution.

In order to evaluate genetic components of variation from these data, a partially hierarchical analysis of variance involving population of origin and sex as main effects and half-siblings as a nested effect within populations was employed (Brownlee, 1960). The interactions of sex by population and of sex by half-sibling nested within population were also analyzed for each measurement. The effect of population of origin was taken into account because the half-siblings used were collected from three different populations, and differences among the populations made a significant contribution to the overall variation in eight of the 12 measurements analyzed.

In this analysis, there are two genetic components of variation that are relevant to the present discussion. The component of variation among half-siblings nested within populations is equal to one-fourth of the additive genetic vari-

TABLE 5. Annual mortality rates for male and female individuals of *Chamaelirium luteum*. Values presented are from 1975–1979 data pooled. Comparisons between male and female mortality rates are based on the log-likelihood ratio (Bishop et al., 1975). n.s. = not significant.

Site	Male Plants	Female Plants	Contrast
Natural Area	3.0	2.6	n.s.
Seawell	1.7	4.0	n.s.
Silver Hill	1.3	5.1	$P < 0.01$

TABLE 6. Mean dry weight and percentage of total dry weight for vegetative and reproductive plant parts for plants harvested in the phytotron experiment.

Character	Male (N = 57)		Female (N = 59)	
	Mean	% of Total	Mean	% of Total
Vegetative				
Rosette Leaves	2.64	46.9	2.98	39.5
Rhizome	1.53	29.3	1.75	24.4
Roots	<u>0.72</u>	<u>14.3</u>	<u>0.99</u>	<u>14.2</u>
Vegetative Total	4.89	90.5	5.72	78.1
Reproductive				
Inflorescence Leaves	0.06	1.3	0.30	4.4
Inflorescence	0.11	2.1	0.25	3.2
Stalk	<u>0.31</u>	<u>6.1</u>	<u>1.01</u>	<u>14.3</u>
Reproductive Total	0.48	9.5	1.56	21.9

ance, which is the portion of the overall variation that is most directly involved with response to selection (Falconer, 1981). In analyses of this type based on field collected progenies, one assumes that maternal effects on the characters measured are negligible and that the female plants have mated at random with male plants in the population. Because the characters assessed in the present study were measured on fully grown individuals, the assumption concerning maternal effects is probably reasonable. Violation of the second assumption would confound attempts to measure the actual level of additive genetic variance; but in the present study we are only concerned with whether or not such genetic variance exists, not with its actual magnitude.

The component of variation attributable to the interaction between sex by halfsibship nested within populations provides a means of evaluating genetic variation in the relative characteristics of male and female plants. In essence the sex by halfsibship interaction represents additive genetic variation for sexual dimorphism.

Analysis of variance (Table 7) showed a strong indication of sexual dimorphism in that differences between the sexes were significant for four of the six dry weight measurements and also for four of the six percentage dry weight measurements. Significant sex by population interactions for rhizome weight and for percent dry weight in rosette leaves and roots indicate that the extent of sexual dimorphism found, at least for vegetative characteristics, is not uniform over the different populations. The observed differentia-

tion among populations suggests further that the extent of sexual dimorphism in resource allocation patterns may be subject to evolutionary modification within particular ecological contexts. However, the characters that showed evidence of additive genetic variation for sexual dimorphism, inflorescence weight, and percentage dry weight of rhizome and inflorescence, are not the same characters that showed a significant sex by population interaction. There were, however, significant levels of additive genetic variation found for rhizome weight, and percentage dry weight of rosette leaves, roots, and inflorescence stalk. The first three of these characters were the characters that did show a significant sex by population interaction. It therefore is reasonable to conclude that the among-population differentiation in the extent of sexual dimorphism is the outcome of the independent responses of male and female plants to site-specific selection pressures.

The manner in which response to selection on a trait in one sex will influence the expression of that trait, and hence the fitness, in the other sex depends on the nature of the genetic correlation that exists between the sexes for that trait. Traits that show a strong genetic correlation, whether positive or negative, between the sexes are not likely to show an independent response to selection on male and female plants because a genetic change that influences the fitness in one sex will also have an influence on the fitness of the other sex. Such genetic correlations have been proposed as a major factor limiting the evolution of

TABLE 7. F-ratio test results^e from the partial hierarchical analyses of variance for plants harvested in the phytotron study.

A. Log Dry Weight		Vegetative			Reproductive			
		df	Rosette	Rhizome ^g	Roots	Inflores-	Inflores-	Stalk
			Leaves ^f			cence		
Population	2	11.6 ^c	3.1 ^d	5.1 ^a	3.3 ^a	2.5 ^d	9.1 ^c	
Sex	1	2.7	3.9 ^d	17.5 ^c	117.1 ^c	12.2 ^c	146.3 ^c	
Sex * Population	2	2.7 ^d	4.9 ^b	0.1	0.2	1.4	2.5 ^d	
Halfsibs within Populations	19	1.2	1.8 ^a	1.6 ^d	0.9	0.4	1.5	
Sex * Halfsibs within Populations	19	1.6 ^d	1.2	1.1	1.0	1.8 ^a	1.2	
Error	72							

B. Arcsin % Dry Weight		Vegetative			Reproductive			
		df	Rosette	Rhizome ^f	Roots ^g	Inflores-	Inflores-	Stalk ^g
			Leaves ^g			cence		
Population	2	2.5	7.2 ^b	3.0 ^d	2.0	1.0	0.4	
Sex	1	35.9 ^c	26.6 ^c	0.1	73.6 ^c	9.9 ^a	122.9 ^c	
Sex * Population	2	3.3 ^a	1.5	6.6 ^c	0.3	0.0	0.6	
Halfsibs within Populations	19	2.5 ^b	1.2	2.1 ^a	1.1	0.3	1.8 ^a	
Sex * Halfsibs within Populations	19	1.5	1.8 ^a	0.9	1.8 ^a	1.7 ^d	1.0	
Error	72							

^a $P < 0.05$.

^b $P < 0.005$.

^c $P < 0.001$.

^d $P < 0.1$.

^e Previously published F-ratios on these data (Meagher & Antonovics, 1982a) were based on non-transformed values of a subset of the data included in the present analyses.

^f When the *sex * halfsibs within populations* mean square was significant, it was used as the denominator in F-ratio tests of *halfsibs within populations*, *sex * population*, and *sex* effects.

^g When the *halfsibs within populations* mean square was significant, it was used as the denominator in the F-ratio test of the *population* effect.

sexual dimorphism (Lande, 1980). A small genetic correlation between the sexes for a given trait, however, would allow independent response to selection in males and females.

Genetic correlations between the sexes (\hat{r}_g) can be estimated from the analysis of variance discussed above using the method of Yamada (1962). For the present analysis,

$$\hat{r}_g = \frac{A - B}{A + B - 2C} \quad (1)$$

where A, B, and C are the mean squares for halfsibships within populations, sex by halfsibships within populations, and error, respectively. Because the data set being analyzed was unbalanced, the estimate \hat{r}_g for the total data set will be biased. In order to reduce this bias and also to provide a standard error of \hat{r}_g for significance

tests, the genetic correlations presented below were estimated using the jackknife method (Gray & Schucany, 1972; see also Rausher, 1984). For this method, estimates of \hat{r}_{gi} , $i = 1, \dots, 22$, were obtained by omitting the i^{th} halfsibship and estimating \hat{r}_g from analysis of the resultant subset of the overall dataset. The reduced bias estimate of \hat{r}_g is then given by

$$\hat{r}_g = N \cdot \hat{r}_g - (N - 1) \cdot \overline{\hat{r}_{gi}} \quad (2)$$

with a standard error of

$$\text{s.e.} = [\sum_i (\hat{r}_{gi} - \hat{r}_g)^2 / N(N - 1)]^{1/2} \quad (3)$$

where N is the number of halfsibships.

Genetic correlations between the sexes were estimated for all of the measured traits that had significant levels of additive genetic variance (Table 8). Significance tests for rosette leaf and

TABLE 8. Genetic correlations (r_g) between the sexes for log dry weight and arcsin % dry weight in vegetative and reproductive structures. The estimates of the correlations and their standard errors were obtained using the jackknife method (Gray & Schucany, 1972); t test results for differences between the estimates and +1, 0, and -1 are also shown.

	Vegetative			Reproductive		
	Rosette Leaves	Rhizome	Roots	Inflorescence		
\hat{r}_g	0.16 ± 0.65	0.57 ± 0.68	-0.32 ± 1.18	-4.19 ± 5.25		
$t_{20} (r_g = +1)$	1.3	0.6	1.1	1.0		
$t_{20} (r_g = 0)$	0.3	0.8	0.3	0.8		
$t_{20} (r_g = -1)$	1.8 ^a	2.3 ^b	0.6	0.6		

	Vegetative			Reproductive		
	Rosette Leaves	Rhizome	Roots	Inflorescence Leaves	Inflorescence	Stalk
\hat{r}_g	0.50 ± 0.40	0.12 ± 0.33	0.97 ± 0.62	0.07 ± 0.58	-32.24 ± 29.43	0.45 ± 1.05
$t_{20} (r_g = +1)$	1.2	2.7 ^b	0.0	1.6	1.1	0.5
$t_{20} (r_g = 0)$	1.2	0.4	1.5	0.1	1.1	0.4
$t_{20} (r_g = -1)$	3.7 ^c	3.4 ^c	2.9 ^c	1.9 ^a	1.1	1.4

^a $P < 0.1$.

^b $P < 0.05$.

^c $P < 0.01$.

rhizome weight and for percent dry weight in rosette leaves, roots, and inflorescence leaves, indicated positive genetic correlations. The genetic correlation between the sexes for percent dry weight in rhizomes was significantly different from both +1 and -1 but not from zero, indicating a low genetic correlation for this trait. The other estimated correlations had such a high variance that no conclusions can be made as to their magnitude or direction.

The presence of positive genetic correlation between the sexes for some traits is hardly surprising; such results imply that the same genes are influencing these traits in both sexes. However, a small genetic correlation, as in the case of percent dry weight in rhizomes, indicates that there is relatively little overlap in the genes regulating that trait in male versus female plants. Therefore the two sexes are capable of independent responses to selection on this trait. The level of resources contained in the rhizome, which probably serves as a storage organ, may well have a direct physiological relationship to the life history differences observed within natural populations, particularly flowering schedules.

CONCLUSION

The ecological consequences of sexual dimorphism in plants are sometimes manifested in the

form of partial spatial segregation between male and female plants along environmental (Freeman et al., 1976) or altitudinal (Grant & Mitton, 1979) gradients or over different microhabitats (Meagher, 1980). If such spatial segregation were taken to extremes, ultimately male and female plants might occur too far apart to effect sexual reproduction. Other ecological consequences of sexual dimorphism that have been observed for some plant species are differences between the sexes in life history characteristics and resource allocation patterns as cited above. Indeed spatial segregation is most likely the result of differential survivorship of male and female plants in different microhabitats (see Meagher, 1980 for review). Other life history dimorphism, such as differences in flowering schedules (Bullock et al., 1982; Meagher, 1981; Vernet, 1971; Valdeyron & Lloyd, 1979) or more specifically in the response to conditions that promote flowering (Meagher, 1981, 1984), might result in a further barrier to interbreeding between male and female plants. For example, such differences in flowering might reduce the probability of simultaneous flowering of male and female plants, or might result in greater spatial separation of simultaneously flowering plants of opposite sex. Yet, in order for a species or population to persist, of course, male and female plants must display suf-

ficient overlap in spatial distribution or flowering behavior to allow reproduction to occur. This is particularly true for plants, which are nonmotile and incapable of the migration during breeding season that occurs in some sexually dimorphic animal species (e.g., Bartholomew, 1970). The limit to the extent of ecological differentiation a species can undergo and still persist thus constitutes an effective limitation on the evolution of sexual dimorphism.

The observed examples of sexual dimorphism in *Chamaelirium luteum* emphasize differences in spatial distribution, life history, and resource allocation, and provide a firm empirical basis for evaluation of the ecological consequences of sexual dimorphism. At the same time, these studies also represent a good start toward understanding ecological constraints on the evolution of sexual dimorphism.

Studies on the genetic basis for resource allocation patterns in the two sexes also provide insight into the evolution of sexual dimorphism. Significant differentiation between the sexes suggests that there has been in the past strong divergent selection on resource allocation patterns in the two sexes. However, male and female plants in a dioecious population share a common genetic heritage; autosomal genes that are present and exposed to selection in one sex will ultimately occur in progeny of the opposite sex. Because genetic changes, or responses to selection, which act to enhance fitness in one sex may conceivably prove to be deleterious to the other sex (Fisher, 1958; Lande, 1980; Yamada & Scheinberg, 1976), this genetic correlation between male and female plants could act to retard divergence between the sexes. Over evolutionary time, strong divergent selection on a particular trait could result in an accumulation of sex-limited gene expression for the genetic loci influencing that trait, thus countering the constraints imposed on the evolution of sexual dimorphism by genetic correlations between the sexes.

Interpretation of the evolution of a set of characters requires an understanding of both the genetic bases for those characters and of the ecological context within which those characters are expressed. Sexual dimorphism in dioecious populations provides an unusually clearcut situation within which to consider ecological and genetic properties of a set of characters simultaneously. By such consideration, we obtain an understanding not only of the type of selective forces acting to promote change in dioecious populations, but

also of the nature of ecological and genetic constraints that act to regulate evolutionary change.

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